Figure 11 Calculated time paths for the response and recovery of the populations (measured in **biomass** Per unit **area, initial** biomass ratios: 50 **phytoplankton:** 10 zooplankton : 1 **small** fish) **in a** three-tiered aquatic food chain when a **-25%** perturbation **in** the **phytoplankton** growth rate is applied at **time zero,** then removed after 3000 days. **"Response"** paths are indicated by right-pointing arrows, and 'recovery' paths are marked **with** left-pointing **arrows. Solid,** dotted, and (partially) dashed lines **give** the paths for **phytoplankton, zooplankton**, and small fish, respectively. Note that the population of small fish **falls** to a critical level and falls to return to Its initial level after 3000 **days** of recovery.

some fraction of the population *remains* after the **stress is** removed.

Figure 12 illustrates that assumptions **as** to the shape of the 'biomass **pyramid"--that is,** the **ratios** of **biomass-per-unit-area** present for each **trophic** level **--can** *have* a profound effect on the magnitude of the **magnification of perturbations down the food** chain from producer to carnivore. Here we show that the effect **of** a -1% change **in** the growth rate of **phytoplankton is** greater on the **fish** population **in** a food chain with biomass ratios **of** 100 : 10 : 1 **(phytoplankton** : zooplankton : fish) than for food chains **in** which the **trophic** level ratios are smaller.   It should be remembered that we know only that this result pertains to the simple **predator-prey** model we have been studying: the effect of the **shape** of biomass pyramids on responses to stress has yet to be investigated for other types of models.

Figure 13 presents the response of the populations in a four-tiered **food-chain** model to a -2% perturbation **in** the growth rate of the **phytoplankton.** Note that, as in the three-tiered case (figure 6) the relative magnitude of changes **in** the populations of the various **trophic** levels increase as the organisms get larger.   Another similarity **is** that the lag In response to the perturbation **is** longer for higher **trophic** levels.   The four-level model does, however, appear to be more stable: a -2% perturbation in r_x **results in** only a 10% decrease **in** the steady-state value of the **larger** fish population, while the highest **trophic** level in the three-tiered case **is** decreased **30% in** population.   In the four-tiered model all four populations oscillate in a damped fashion toward a steady state value.   **This** is the sort of behavior that one might expect from a real ecosystem.   It **is** also gratifying to note that the oscillations in the populations of each predator-prey pair are out of phase with each other.   This makes ecological as well as mathematical sense. As the population *of* larger fish, for example, declines, grazing pressure on small fish decreases, allowing that population to expand.   This increase in
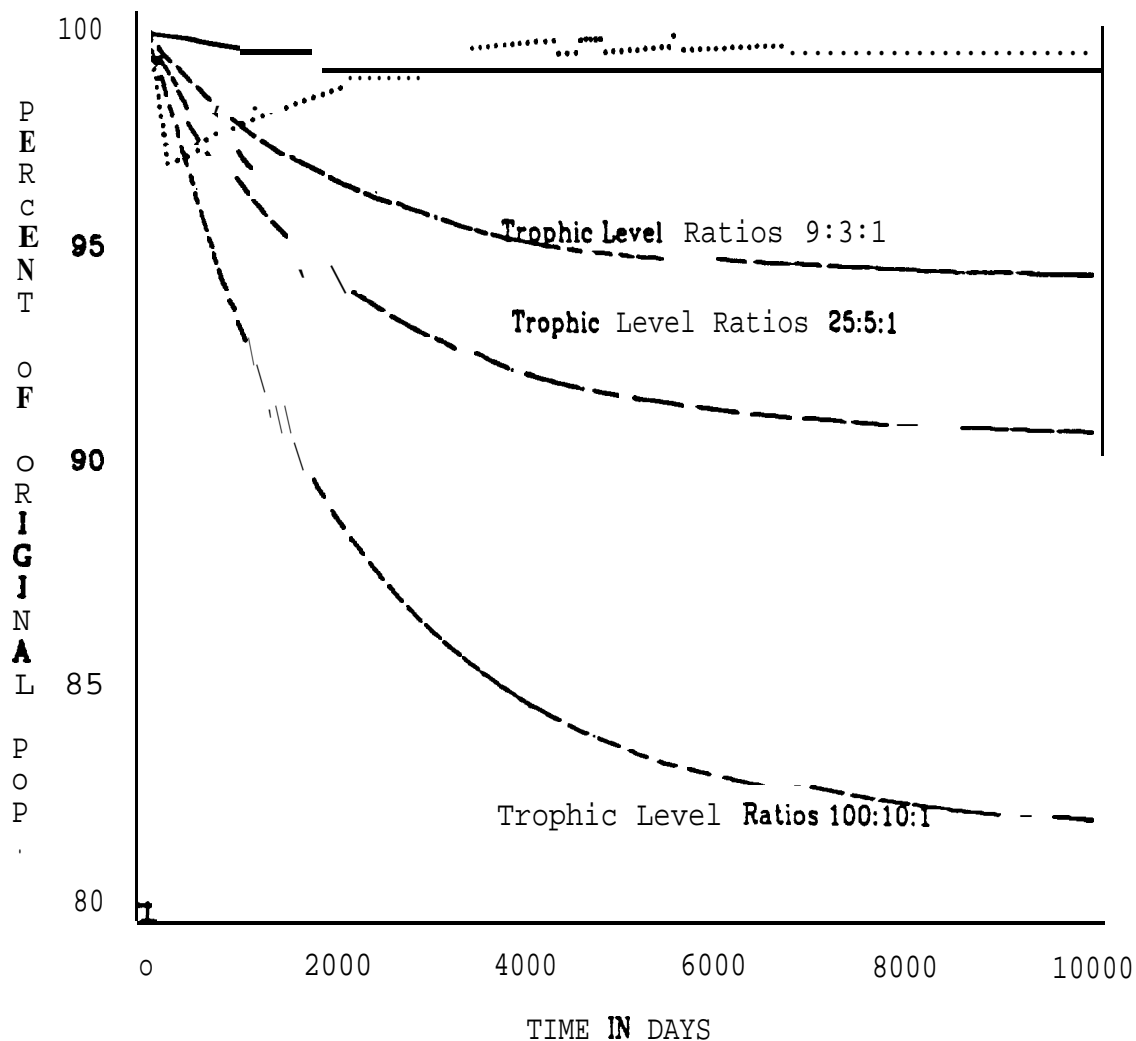
Figure 12 The response of three different three-tiered aquatic ecosystems to a -1% change in the phytoplankton growth rate. The partially dashed curves give the response of the small fish populations to the perturbation for food chains in which the initial biomass ratios (per-unit-area biomass of phytoplankton: zooplankton: small fish) are as indicated. The solid and dashed lines give the response of phytoplankton and zooplankton populations for a food chain with 100:10:1 biomass ratios.
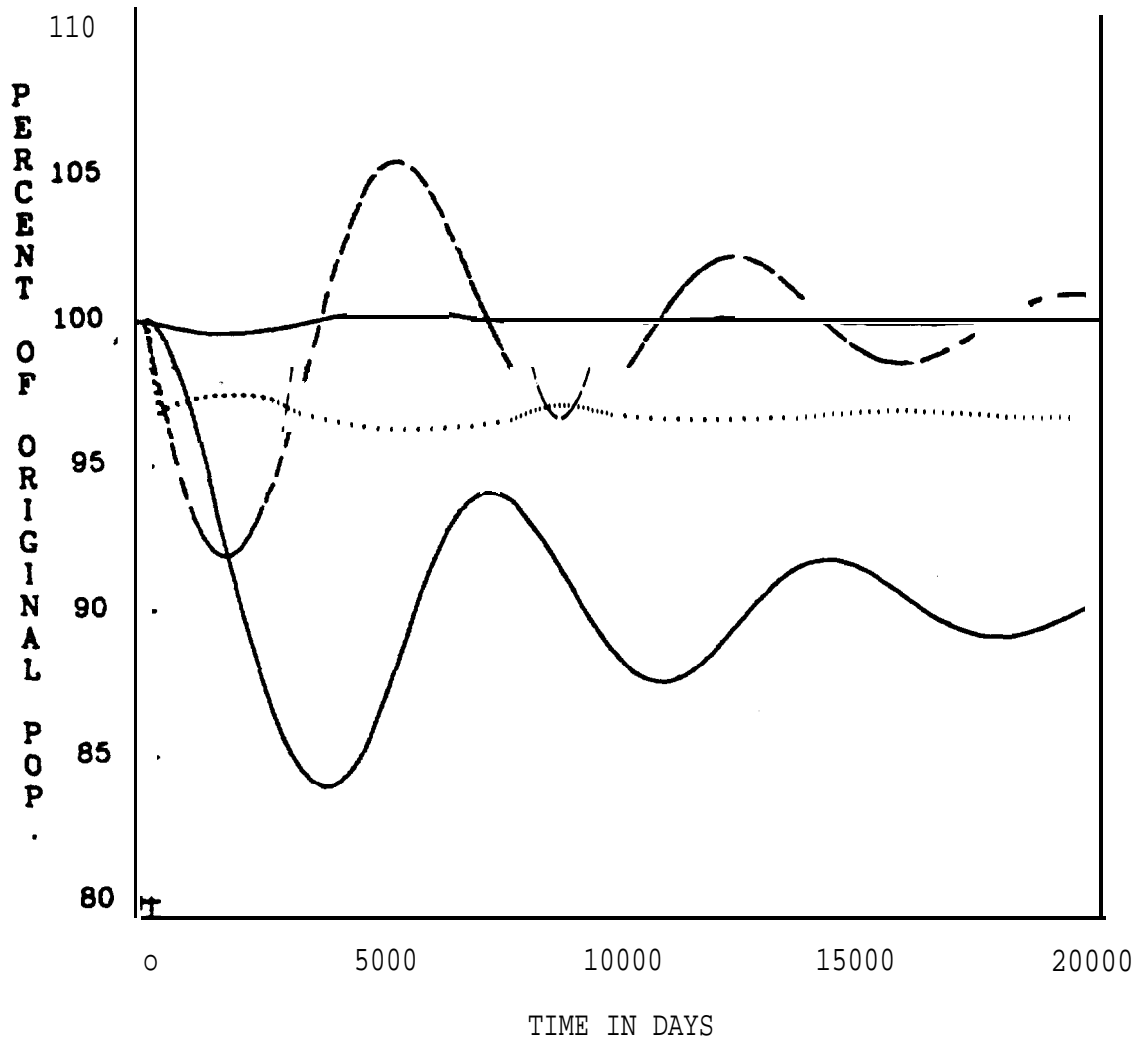
Figure 13   The response of the populations in a four-tiered aquatic
ecosystem (measured in biomass per unit area, initial biomass
ratios: 500 phytoplankton: 100 zooplankton : 10 small fish: 1
larger fish) to a -2% perturbation in the phytoplankton growth
rate.   The paths for the responses of the phytoplankton,
zooplankton, small fish, and larger fish population are given
by the upper solid curve, the dotted curve, and partially
dashed curve, and the lower solid curve, respectively.

small fish creates favorable conditions for the larger fish, which multiply until the small fish have been overgrazed. At this point the population of larger fish starts to decline, the small fish start to increase, and the cycle starts again.

Figures 14 and 15 show the response of the four-tiered ecosystem to a -2% changes in r_x, and chart recovery paths for cases in which the perturbation is removed after 2000 and 4000 days, respectively. These two figures illustrate how important the timing of the removal of a stress can be. When the stress is removed after 2000 days there is a pronounced lag in the return path of the larger fish population. After 2000 days of recovery that population is still less than its pre-perturbation level. If the stress is removed after 4000 days, the population of larger fish returns to its original level after 2000 days, and is actually 10% above its original level after 4000 days of recovery. This does not imply, certainly, that it would be prudent to delay the clean-up of a polluted aquatic ecosystem in the hopes that recovery will be faster If one waits longer; it merely Illustrates that the recovery of a perturbed ecosystem may not be a simple monotonic function of the length of time over which it has been polluted.

Our mathematical models tend to validate both the ideal and non-ideal theoretical hysteresis models. Lower trophic levels tend to return to their original levels after a relatively short recovery time, and thus show ideal hysteresis. For higher trophic levels (and especially with more severe stresses) the non-ideal hysteresis model dominates: larger organisms respond to a stress more slowly and recover more slowly, and frequently fail to return to their initial positions within a time-frame relevant to policy decisions. We should note, however, that by the nature of the mathematics used all of the populations we have modelled will eventually return to their original levels, given a sufficiently long recovery period.
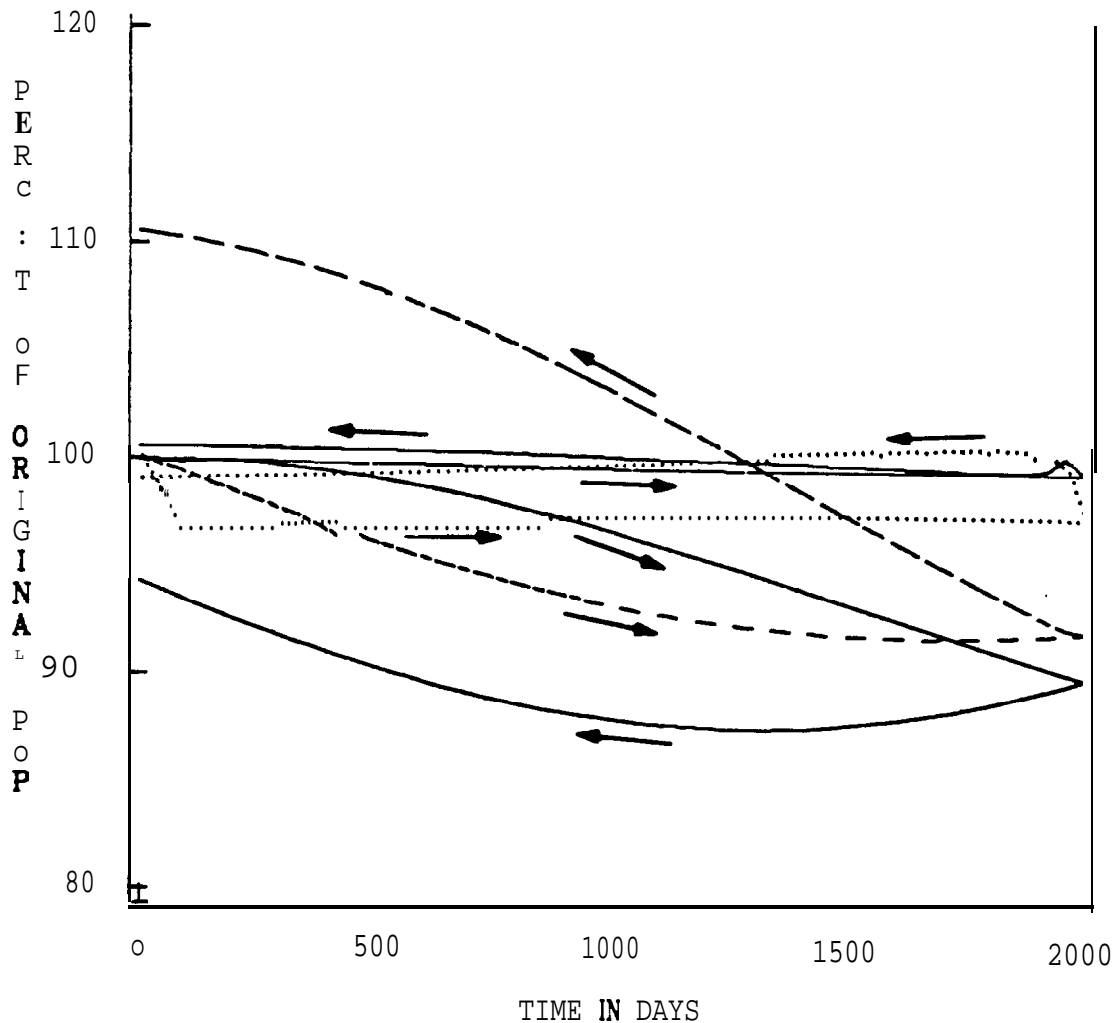
Figure 14   Calculated time paths for the response and recovery of the
populations in a four-tiered aquatic ecosystem (measured in
biomass per unit area, initial biomass ratios: 500
phytoplankton: 100 zooplankton : 10 small fish: 1 larger fish)
to a -2$ perturbation in the phytoplankton growth rate applied
at time zero and removed after 2000 days.   'Response" paths
are indicated by right-pointing arrows, and 'recovery* paths
are marked with left-pointing arrows.   The paths for the
responses of the phytoplankton, zooplankton, small fish, and
larger fish populations are given by the upper solid curves,
the dotted curves, the partially dashed curves, and the lower
(more highly arched) solid curves, respectively.   Note that
the population of larger fish falls to return to its original
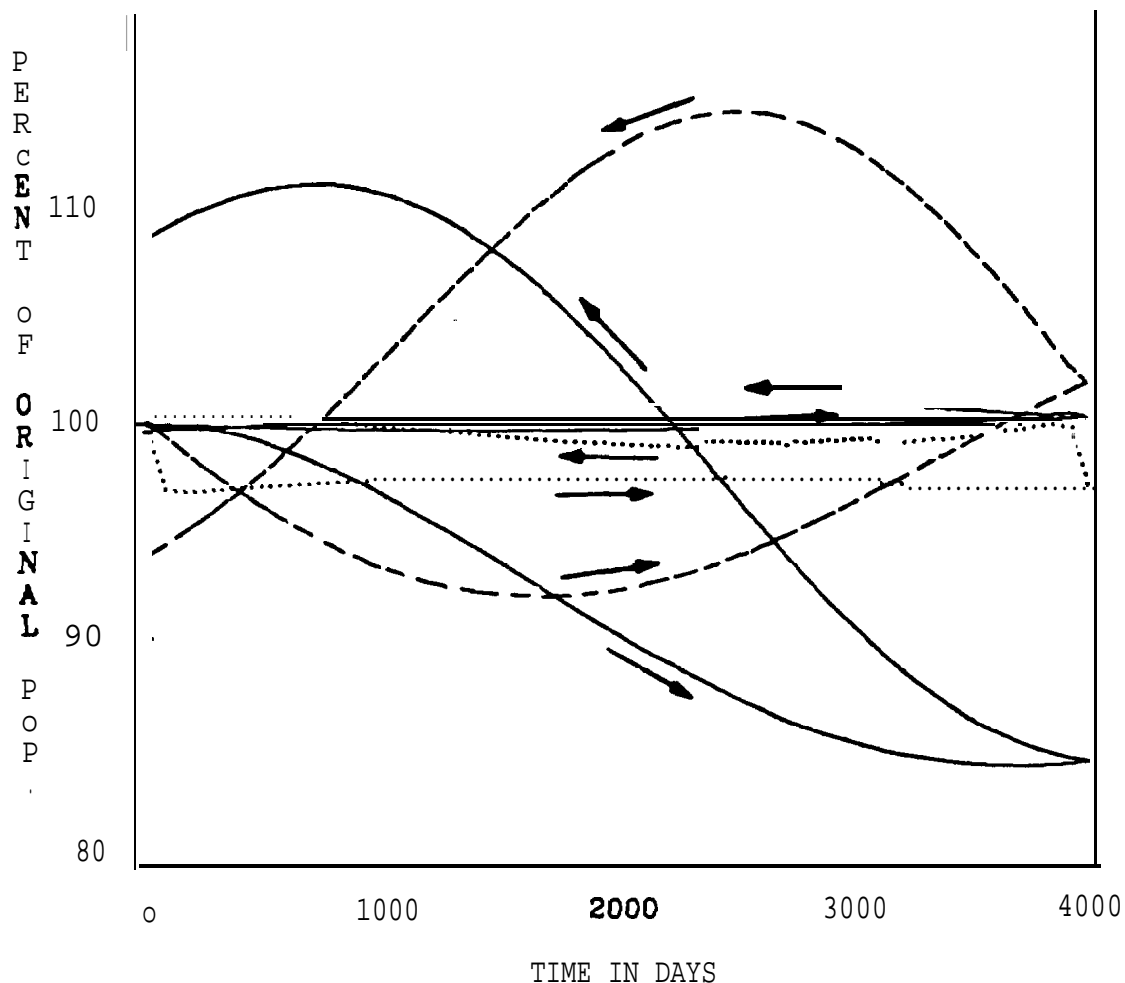position after 2000 days of recovery.

Figure 15   Calculated **time paths** for the response and recovery of the
populations **in a** four-tiered aquatic ecosystem (measured **in**
biomass per unit area, initial **biomass** ratios: 500
phytoplankton: 100 zooplankton : 10 **small** fish: 1 larger fish)
to a **-2%** perturbation **in** the **phytoplankton** growth rate applied
at time zero and removed after **4000** days.   **"Response" paths**
are indicated by right-pointing **arrows,** and 'recovery" paths
are marked **with** left-pointing arrows.   The paths for the
responses of the **phytoplankton, zooplankton,** small **fish,** and
larger **fish populations** are given by the upper **solid** curves,
the dotted curves, the partially **dashed** curves, and the lower
(more highly arched) **solid** curves, respectively.   Note that
the population of larger **fish** returns to **its** original position
after 2000 days of recovery and actually **overshoots its**
level by **4000** days after the perturbation is removed.

30

We expect that the addition of higher trophic levels including larger, longer-lived organisms will show the non-ideal hysteresis model to be more useful for population changes occuring within a time-frame relevant to policy-making.

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Discussion

Mathematical models of ecosystem perturbations are often used in ecology (Patten, 1975; O'Neill, 1976) and aquatic ecology (O'Melia, 1972; Bierman et al, 1980; Inoue et al, 1981). The drawbacks of such models are now sufficiently well understood as to allow for their restricted use.

Our mathematically-derived curves for the pollution and recovery of an aquatic ecosystem demonstrate a hysteresis effect. These curves agree closely with the ideal and non-ideal conceptual hysteresis models described above. We can use the information in our mathematically-derived curves to choose which of the conceptual models is more realistic.

The non-ideal conceptual model selected by this process is of great interest since it forecasts that the most economically valuable species, such as commercial and sports fish, will not directly and reversibly return to their original levels. This is due to the time lags that come about in part because organisms in higher trophic levels are slower to multiply and in part because increases in these levels must follow recovery of their prey populations. This type of sustained hysteresis effect is apparently inherent in ecosystems including linked trophic levels.

Our model differs from many perturbation models (e.g. O'Neill, 1976) in that we have assumed that the disturbance caused by pollution is small but continuous. This kind of small change is to be expected from 'modern" pollution, where sophisticated treatment of waste is mandated and disposal of the end product of the treatment process cannot be postponed or diverted.

Sewage and Industrial-waste effluents from large **cities** or companies are examples of such **waste** streams. Similarly, **it is** unlikely that total restoration of a grossly polluted ecosystem would be considered. Rather, a **small** upgrading (**e.g.** through control of point-sources of **toxic** metals, a decrease **in** suspended solids, or a reduction **in** chlorine loading) of a partially restored or partially damaged system **is** envisaged, as opposed to a **massive** ecological change. This sort of approach **is** typical of **pollution-**control strategies currently used **in** the U.S.

There are, **however,** two potential drawbacks to our simple mathematical **model.** First, pollution-induced changes **in** real aquatic ecosystems are unlikely to be quite as steady and continuous as we have modeled **them.** For example, many fish scarcely feed over the winter, and are thus unaffected by decreases in algae or zooplankton populations over that time period. Second, our model predicts that small fish will rather quickly be forced nearly to extinction If larger (e.g. 2S%) continuous depressions of primary production are used. This **is** probably unrealistic due to the patchy nature of the seasonal and spatial distribution of food for **higher-trophic-level** organisms. **We** expect that some clarification of these drawbacks will result from our future comparisons of the simple **Trophic-Link Model** (three **trophic** and four levels) with a five-level version, and the comparison of both of these with real data (yet to be assembled).

Our deterministic **TLM** may also be insensitive to other likely ecosystem stresses that are stochastic **in** nature. A cool spring and summer may, for example, result **in** the year's juvenile fish crop being undersized at the end of the growth season, leaving them more vulnerable to **cannibalism** overwinter (Kipling, 1976). How would such a random event affect the hysteresis **loops** we have modeled, especially in the recovery phase? **In** progressing from a

deterministic to a Stochastic model **ling** approach, the **major** difference we would anticipate **would** be that the position of the **system** would be described in probabilistic terms.   **For** example, with respect to the -25$ perturbation **shown** in figure 11, instead of the small fish population becoming critically **low** after 3000 days with a probability of one, it might do so with a probability of **0.9,** and have an additional probability of 0.1 of becoming critical at some other time.   **Ginzburg** et al (1982) present a methodology for obtaining such extinction probabilities within the framework of a stochastic single-species population model.   We intend to consider whether a similar approach is feasible for a multi-species model with realistic parameters.

We realize that the results of the **HTLM** are dependent on the form of the different differential equations used, the values **chosen** for the parameters, the method **of** solution of the equations, and the functional components **of** the ecosystem that the model describes.   We intend, **in** fact to examine how changes **in** the form and parameters of **HTLM's** affect the results of such models.   While no one **trophic** link model can predict the behavior of a variety of ecosystems or even one specific ecosystem, with great certainty, we hope that advanced forms of the **HTLM** can be developed that **can, when properly** specified and calibrated with field data from a **specific ecosystem,** yield meaningful insights into the future behavior of that ecosystem **in** response to pollutant stresses.   This does <u>not</u> mean that we believe any such model can be used to definitively predict that reducing the annual loading of compound X by 100 tons per year **will** result in a **5.5% increase in the number** of game fish.   The appropriate use for a properly calibrated ❑odel would be **as** an aid in making the type of yes/no choices that regulators often face. Suppose, for example, that a regulator wished to know whether or not to order the clean-up of a specific lake.   If a carefully constructed and calibrated HTLM indicated that a substantial fraction of the population of an important

game fish would be likely to be lost if clean-up were delayed, the regulator might, after weighing the evidence, decide to proceed with pollution abatement. In such a case it would not matter if the model predicted a 40%, 60%, 80%, or 100% reduction in fish: the conclusion drawn by the regulator would be the same.

We feel that the simplicity of the HTLM framework will make it possible to easily calibrate models for specific situations. These models could then be run to yield qualitative information that, because of the simplicity of the models, can be traced back to allow a better understanding of the ecology behind the result.

summary

Our initial results suggest that the hysteresis effect may be one reason why some valuable fisheries resources (e.g. the Great Lakes, where sports fisheries have failed to re-establish themselves following pollution control efforts) thave failed to respond to reduction in pollution. An understanding of hysteresis phenomena may also make it possible to predict (in an approximate way) how long it will take to see a recovery of a fish resource. An equally important application of the concept is to use it to gain a qualitative feeling for why some components of ecosystems and not others fail to show ideal hysteresis behavior and consequently become locally extinct. Further calculations using more trophic levels, different values for key parameters, and generation times derived from data on natural ecosystems, may show how useful the hysteresis concept can be for economic evaluation of pollution-control benefits that may be long delayed by ecosystem hysteresis.

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APPENDIX : <u>**DETAILS**</u> OF <u>**MATHEMATICS**</u>

DETAILS OF MATHEMATICS

ASSUMPTIONS FOR THREE-LEVEL MODEL:

$$dX/dt = r_x X(1 . X/K_x) - B_{xy}XY - b_x X$$

$$dY/dt = E_{xy}B_{xy}XY - B_{yz}YZ - b_y Y$$

$$dZ/dt = E_{yz}B_{yz}YZ - b_z Z;$$

X = Phytoplankton, Y = Zooplankton, Z = Small Fish;

Steady-State Populations: $X^* = 50$, $Y^* = 10$, $Z^* = 1$;

$E_{xy} = 0.1$, $E_{yz} = 0.1$, $K_x = 100$;

Generation Times: $T_x = 3$ days, $T_y = 20$ days, $T_z = 360$ days.

$$T_x = r_x^{-1}, \quad T_Y = (E_{xy}B_{xy}X^*)^{-1}, \quad T_z = (E_{yz}B_{yz}Y^*)^{-1}$$

so...

$$r_x = (T_x)^{-1} = (3)^{-1} = 1/3,$$

$$B_{xy} = 1/T_y E_{xy} X^* = (20 \times 0.1 \times 50)^{-1} = 10^{-2},$$

$$B_{yz} = 1/T_z E_{yz} Y^* = (360 \times 0.1 \times 10)^{-1} = 1/360.$$

At Steady-State:

$$r_x X^*(1 - X^*/KX) - B_{xy}X^*Y^* - b_x X^* = 0$$

$$E_{xy}B_{xy}X^*Y^* - B_{yz}Y^*Z^* - b_y Y^* = 0$$

$$E_{yz}B_{yz}Y^*Z^* - b_z Z^* = 0.$$

so...

$$b_x = (1/3)(1 - 1/2) - (10^{-2} \times 10) = 1/6 - 0.1 = .0666667$$

$$b_y = (0.1 \times 10^{-2} \times 50) - (1/360) = 0.05 - 1/360 = 0.04722$$

$$b_z (0.1 \times 1/360 \times 10) = 1/360.$$

ASSUMPTIONS FOR FOUR-LEVEL MODEL:

$$dX/dt = r_x X(1 - X/K_x) \cdot B_{xy}XY - b_x X$$

$$dY/dt = E_{xy}B_{xy}XY - B_{yz}YZ - b_y Y$$

$$dZ/dt = E_{yz}B_{yz}YZ - B_{zf}ZF - b_z Z$$

$$dF/dt = E_{zf}B_{zf}ZF - b_f F;$$

x = Phytoplankton, Y = Zooplankton, Z = Small Fish, F = Larger Fish;

Steady-State Populations: $X^* = 500$, $Y^* = 100$, $Z^* = 10$, $F^* = 1$;

$E_{Xy} = 0.1$, $E_{yz} = 0.1$, $E_{zf} = 0.1$, $K_x = 1000$;

Generation Times: $T_x = 3$ days, $T_y = 20$ days, $T_z = 360$ days, Tf = 1080 days.

$T_x = r_x^{-1}$, $T_Y = (E_{xy}B_{xy}X^*)^{-1}$, $T_z = (E_{yz}B_{yz}Y^*)^{-1}$, and $T_f = (E_{zf}B_{zf}Z^*)^{-1}$

so...

$$'_x = (T_x)^{-1} = (3)^{-1} = 1/3,$$

$$B_{xy} = 1/T_y E_{xy}X^* = (20 \times 0.1 \times 500)^{-1} = 10^{-3},$$

$$B_{yz} = 1/T_z E_{yz}Y^* = (360 \times 0.1 \times 100)^{-1} = 1/3600, \text{ and}$$

$$B_{zf} = 1/T_f E_{zf}Z^* = (1080 \times 0.1 \times 10)^{-1} = 1/1080.$$

At Steady-State:

$$r_x X^*(1 - X^*/K_x) - B_{xy}X^*Y^* - b_x X^* = 0$$

$$E_{xy}B_{xy}X^*Y^* - B_{yz}Y^*Z^* - b_y Y^* = 0$$

$$E_{yz}B_{yz}Y^*Z^* - B_{zf}Z^*F^* - b_z Z^* = 0, \text{ and}$$

$$E_{zf}B_{zf}Z^*F^* - b_f F^* = 0.$$

so...

$$b_x = (1/3)(1 - 1/2) - (10^{-3} \times 100) = 1/6 - 0.1 = .0666667$$

$$b_y = (0.1 \times 10^3 \times 500) - (1/3600 \times 10) = 0.05 - 1/360 = 0.04722$$

$$b_z (0.1 \times 1/3600 \times 100) - (1/1080) = 1/360 - 1/1080 = 1/540, \text{ and}$$

$$b_f (0.1 \times 1/1080 \times 10) = 1/1080.$$

```
c          This program, which incorporates the NAG subroutine do2ebf, can
c          be used to solve three coupled differential equations.
c            ..scalars in common
           implicit double precision (a-h, o-z)
           double precision H, xend
           integer 1
c            ...
c            ..local scalars..
           double precision tol, x
           integer Ifail, IR, IW, roped, nout
c            ..local array s..
           double precision W(3,21), Y(3)
c            ..subroutine references.,
c          d02ebf
c            ..
           external fen, out, pederv
           common xend, H, I
           open(8, file= 'output')
c          opens file, named "output", in which results are to be placed
           data nout /$/
           write (nout,99996)
           write (8,99996)
           write (nout,99994)
           write (8,99994)
           N = 3
           IW = 21
           MPED = O
           I R = 2
           tol = 10.0d0**(-5)
           write (nout,99999) tol
           write (nout,99998)
           write (8,99999) tol
           write (8,99998)
           x = 0
           xend = 1.0d4
c          Program is now set to calculate a "response" path. To calculate a
c          "return" path one would substitute post-perturbation values for
c          y(1-3) below
           y(1) = 50.0d0
           y(2) = 10.0d0
           y(3) = 1.0d0
           H = (xend-x)/50
c          Prints out solution at 49 evenly spaced points between x(0) and xend
           1 = 49
           Ifail = 1
           call D02EBF(x, xend, N, y, tol, IR, fen, roped, pederv,
          .out, W, IW, Ifail)
           write (nout,99997) Ifail
           write (8,99997) Ifail
```

```fortran
      subroutine pederv(x, y, PW) ·
c        ..scalar arguments..
      double precision x
c        ..array arguments..
      double precision PW(3,3), y(3)
c        ..
      PW(1, i) = -1.00 d0*2.0d0*(1.0d0/( 3.0d0*100.0d0)) -y(1) +
     + + 1.00d0*(1.0d0/3 .0d0) - 0.06666666666666667d0
     + - (1. 0d0/100.0d0)*y(2)
      PW(1,2) = (1. 0d0/100.0d0)*y(1)
      PW(1,3) = 0.0d0
      PW(2,1) = (1.0d0/100.0d1) *y(2)
      PW(2,2) = -(1. 0d0/36.0d1)*y(3) - (4.72222222222d-2) +
     + (1. 0d0/100.0d1)*y(1)
      PW(2,3) = -(1. 0d0/36.0d1)*y(2)
      PW(3,1) = 0.0d0
      PW(3,2) = (1.0d0/36.0d2)*y(3)
      PW(3,3) = (1. 0d0/36.0d2)*y(2) - 1.0000 d0*(1.0d0/3.6d2)
      return
      end
      subroutine out(x, y)
c        ..scalar arguments..
      double precision x, u
c        ..array arguments..
      double precision y(3)
      double precision z(3)
c     u allows time to be counted "backwards" (for return paths), while z(3)
c     is a set of variables that allow the populations, y(t), to be normalized
c     with respect to one another.  The equations for 2(1-3) below express
c     each y(t) as a percentage of the initial population in that trophic level
c
c        ..scalars in common..
      double precision H, xend
      integer-1
c
c        ..local scalars..
      integer J, nout
c
      common xend, H, I
      data nout ./6/
      z(1) = y(1)/0.5d0
      z(2) = y(2)* 10.0d0
      z(3) = y(3)* 1.0d2
      u = 1.0d4 - x
      write (nout,99999) x, (z(J),J= 1,3)
      write (8,99999) x, (z(J), J=1,3)
      x = xend - dble(I)*H
      I = I-1
      return
99999 format (1H , F8.2,3E13.5)
      end
```

```fortran
      If (tol.lt.o) write (nout,99995)
      If (tol.lt.o) write (8,99995) .
   20 continue
      roped = 1
c     roped = 1 indicates that routine is using supplied Jaccccccc (in PEDERV)
c     rather than calculating it internally (which happens wwww mped = 0)
      write (nout,99993)
      write (8,99993)
      tol = 10.0d0**(-5)
      write (nout,99999) tol
      write (8,99999) tol
      write (8,99998)
      write (nout,99998)
      X = o
      xend = 1.0d4
      y(1) = 50.0d0
      y(2) = 10.00d0
      y(3) = 1.0d0
      H = (xend-x)/50
      I = 49
      Ifail = 1
      call D02EBF(x, xend, N, y, tol, IR, fen, roped, pederv,
     •out, W, IW, Ifail)
      write (nout,99997) Ifail
      If (tol.lt.o) write (nout,99995)
      write (8,99997) Ifail
      If (tol.lt.o) write (8,99995)
   40 continue
      stop
99999 format (22hOCALCULATION WITH TOL=, e8. 1)
99998 format (40h T AND SOLUTION AT EQUALLY SPACED POINTS
99997 format (8h Ifail= 11)
99996 format (4(1x/), 3 1h D02EBF EXAMPLE PROGRAM RESULTS  x)
99995 format (24h RANGE TOO SHORT FOR TOL)
99994 format (32hOCALCULATING JACOBIAN INTERNALLY)
99993 format (31hoCALCULATING JACOBIAN BY PEDERV)
      end
      subroutine fcn(T, y, F)
c     ..scalar arguments..
      double precision T
c     ..array arguments..
      double precision F(3). y(3)
c     ..
      F(1) = 1.00d0*(1.0d0/3.0d0)*y(1)*(1.0d0-(y(1)/100.0dC .-
     + (1. 0d0/100.0d0)*y(1)*y(2)
     + - 0.066666666666667 d0*y(1)
      F(2) = (1.0d0/100.0d1) *y(1) •y(2) - ((1.0d0/36.0d1)*y(2)     ))-
     + (4.72222222222 d-2)*y(2)
      F(3) = (1.0d0/36.0d2)*y(2)*y(3) - 1.00d0*(1.0d0/3.6d2)
c     program is now set at steady state. To model a perturbation
c     in the phytoplakton growth rate, replace "1.00d0" in the  ression
c     for F(1) (and also in the expression for PW(1. 1), below)
c     with, for example, "0.98d0" (for a 2% decrease)
      return
      end
```

LISTING *OF* COMPUTER PROGRAM USED TO CALCULATE TIME PATHS FOR

FOUR-LEVEL, AQUATIC ECOSYSTEM MODEL

```
c        .. Scalars in common
      implicit double precision (a-h, o-z)
      double precision H, xend
      integer I
c       .,.
c       ..local scalars..
      double precision tol, x
      integer Ifail,IR,IW, roped, nout
c       ..local array s..
      double precision W(4,22), y(4)
c       ..subroutine references..
c       d02ebf
c          . .
      external fen, out, pederv
      common xend, H, 1
      open(8, file='output')
c       Places the output of this program into a file named "output"
      data nout /6/
      write (nout,99996)
      write (8,99996)
      write (nout,99994)
      write (8,99994)
      N = 4
      IW = 22
      MPED = O
      IR = 2
      tol = 10. 0d0**(-5)
      write (nout,99999) tol
      write (nout,99998)
      w-rite (8,99999) tol
      write (8,99998)
      X = o
c       Program is now set to calculate time paths starting with steady-state
c       conditions.  To calculate "return" paths, replace the values of
c       y(1-3) below with post-perturbation values
      xend = 2.0d4
      y(1) = 500.0d0
      y(2) = 100.0d0
      y(3) = 10.0d0
      y(4) = 1.0d0
      H = (xend-x)/50
      I = 49
      Ifail = 1
      call D02EBF(x, xend, N, y, tol, IR, fen, roped, pederv,
     .out, W, IW, Ifail)
      write (nout,99997) Ifail
      write (8,99997) Ifail
      If (tol.lt.o) write (nout,99995)
      If (tol.lt.o) write (8,99995)
   20 continue
c       This section. which is optional, calculates time points based on values
c       of the Jacobian matrix of the system supplied in "PEDERV", below
      roped = 1
      write (nout,99993)
      write (8,99993)
```

A-6

```fortran
      tol = 10.0d0**(-5)
      write (nout,99999) tol
      write (8,99999) tol
      write (8,99998)
      write (nout,99998)
      x = 0
      xend = 2.0d4
      y(1) = 500.0d0
      y(2) = 100.0d0
      y(3) = 10.0d0
      y(4) = 1.0d0
      H = (xend-x)/50
      I = 49
      Ifail = 1
      call D02EBF(x, xend, N, y, tol, IR, fen, roped, pederv,
     .out, W, IW, Ifail)
      write (nout,99997) Ifail
      If (tol.lt.o) write (nout,99995)
      write (8,99997) Ifail
      If (tol.lt.o) write (8,99995)
   40 continue
      stop
99999 format (22hCALCULATION WITH TOL=,e8.1)
99998 format (40h T AND SOLUTION AT EQUALLY SPACED POINTS)
99997 format (8h lfail= 11)
99996 format (4(1x/),31h D02EBF EXAMPLE PROGRAM RESULTS/lx)
99995 format (24h RANGE TOO SHORT FOR TOL)
99994 format (32hCALCULATING JACOBIAN INTERNALLY)
99993 format (31hCALCULATING JACOBIAN BY PEDERV)
      end
      subroutine fcn(T, y, F)
c        ..scalar arguments..
      double precision T
c        ..array arguments..
      double precision F(4), y(4)
c        ..
c     To calculate response to a perturbation in the phytoplankton growth rate,
c     replace "1.00d0" in F(1), and PW(1, 1) below with, for example "0.98d0"
c     (for a -2% perturbation
      F(1) = 1.00d0*(1.0d0/3.0d0)*y(1)*(1.0d0-(y(1)/100.0d1)) -
     + (1.0d0/100.0d1)*y(1)*y(2)
     + - 0.066666666666667 d0*y(1)
      F(2) = (1.0d0/100.0d2)*y(1)*y(2) - ((1.0d0/36.0d2)*y(2)*y(3)) -
     + (4.72222222222 d-2)*y(2)
      F(3) = (1.0d0/36.0d3)*y(2)*y(3) - ((1.0d0/1080.0d0)*y(3)*y(4)) -
     + 1.00d0*(1.0d0/5.4 d2)*y(3)
      F(4) = (1.0d0/1080.0d1)*y(3)*y(4) - ((1.0d0/1080.0d0)*y(4))
      return
      end
```

```fortran
      subroutine pederv(x, Y, PW)
c        ..scalar arguments..
      double precision x
c        ..array arguments..
      double precision PW(4,4), y(4)
c        ..
      PW(1,1) = -1.00 d0*2.0d0*(1.0d0/(3.0d0*100.1d0))*y(1) +
     + + 1.00d0*(1.0d0/3.0d0) - 0.06666666666666667d0
     + - (1. 0d0/100.0d1)*y(2)
      PW(1,2) = (1. 0d0/100.0d1)*y(1)
      PW(1,3) = 0.0d0
      PW(1,4) = 0.0d0
      PW(2,1) = (1. 0d0/100.0d2)*y(2)
      PW(2,2) = -(1. 0d0/36.0d2)*y(3) - (4.72222222222d-2) +
     +   (1. 0d0/100.0d2)*y(1)
      PW(2,3) = -(1. 0d0/36.0d2)*y(2)
      PW(2,4) = 0.0d0
      PW(3,1) = 0.0d0
      PW(3,2) = (1.0d0/36.0d3)*y (3)
      PW(3,3) = (1. 0d0/36.0d3)*y(2) - 1.00d0*(1.0d0/5.4d2) -
     +   (1.0d0/1080.0d0) *y(4)
      PW(3,4) = (1. 0d0/1080.0d0)*y(3)
      PW(4,1) = 0.0d0
      PW(4,2) = 0.0d0
      PW(4,3) = (1. 0d0/1080.0d1)*y(4)
      PW(4,4) = (1. 0d0/1080.0d1)*y(3) - (1. 0d0/1080.0d0)
      return
      end
      subroutine out(x, y)
c        ..scalar arguments..
      double precision x, u
c        ..array arguments..
      double precision y(4)
      double precision z(4)
c     "u" allows time to be counted "backwards" for return time paths: 2(1-4)
c     is a set of variables that allow the time points for y(1-4) to be
c     expressed as percentages of the initial populations in each trophic
c     level
c        ..
c        ..scalars in common..
      double precision H, xend
      integer I
c        ..
c        ..local scalars..
      integer J, nout
c        .,
      common xend, H, I
      data nout /8/
      z(1) = y(1)/0.5d1
      z(2) = y(2)
      z(3) = y(3)* 1.0d1
      z(4) = y(4)* 1.0d2
      U = 2.0d3 - X
      write (nout,99999) u, (z(J), J=1,4)
      write (8,99999) u, (z(J), J=1,4)
      x = xend - dble(I)*H
      I = I - 1
      return
99999 format (1H , F8.2, 4E13.5)
      end
```